Annulus Formation on Scales of Four Species of Coregonids Reared Under Artificial Conditions[1,2]

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ABSTRACT

Scales from known-age coregonids reared in the laboratory were examined to determine when annuli formed and to learn possible factors of their formation. Scales were taken monthly from marked fish for periods up to 21 months. Scales were also examined from fish that died and from preserved specimens of young-of-the-year for each species. Two marks formed on almost all scales each calender year. The stronger formed during March–April and the weaker in October–November. Both marks had all the usual characteristics of an annulus but the spring mark was considered the annulus and the fall mark an accessory check. The annulus formed during a period of constant temperatures and of little change in growth or increasing growth. The accessory check formed during a period of declining temperatures (1–5 degrees F, or 0.6–2.8 degrees C, per month) and of little change in growth or declining growth. Most fish grew throughout the winter; the only exceptions were one bloater (*Coregonus hoyi*) and several of the largest lake whitefish (*C. clupeaformis*). Fish were always given all the food they would eat to eliminate availability of food as a factor of mark formation. The temperature of the water during the winter (50 ± 0.3 F; 10.0 ± 0.2 C) did not arrest metabolic activity. The growth rate was related more closely to day length than to other variables examined.

INTRODUCTION

This study is based on scales from known-age coregonids (lake whitefish and ciscoes) reared at the U.S. Bureau of Commercial Fisheries Biological Station at Northville, Michigan. The study was initiated to determine if the fish formed annuli, and to find possible relationships between annulus formation and environmental conditions.

Van Oosten (1923) established the time of annulus formation for lake whitefish (*Coregonus clupeaformis*) reared in aquariums and later (1929) made a critical evaluation of the scale method for age determination of the lake herring (*C. artedi*) of Lake Huron. The basic assumptions inherent in the scale method and the views on factors of annulus formation developed by Van Oosten are mostly held valid today. The present study indicated, however, that length of day, not previously thought to influence annulus formation, may be an important factor for the coregonids.

Life histories have been studied for at least one population of most species of coregonids of the Great Lakes, but few of the studies established the time

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of annulus formation and none included experimental data on the formation of the marks used to estimate age and calculate growth. Evidence is provided here which emphasizes the need for careful validation of the year-mark on some populations of wild coregonids.

MATERIALS AND METHODS

The three species and one hybrid investigated were lake whitefish, bloater, kiyi (*C. kiyi*), and the first generation of a cross between female lake herring and male bloater.

In June or early July 1962, the largest fish in each of nine tanks, each containing various year-classes and species, was anesthetized, inoculated with antibiotics, measured, and injected with experimental orange dye (composition unknown to me). In September 1962, three young-of-the-year whitefish were similarly marked. Each month (with few exceptions) one or two scales were taken from the left side of each marked fish, between the dorsal fin and lateral line. If a marked fish died, the next largest fish in that tank was marked and a new series was started.

Scales were taken from 16 marked fish, including at least two individuals of each species and the hybrid (Table I). The number of scale samples from individual fish ranged from 3 to 17 over periods up to 21 months. A total of 137 scale samples from the marked fish was examined.

Scale samples were also obtained from unmarked fish that shared the tanks with the marked ones. When a fish died it was measured, labeled, and preserved. Scales for study were removed from two or three fish of each species that died each month through 1963. Scales from young-of-the-year of each species were also examined to determine scale development before the first annulus. A total of 288 scale samples from unmarked fish was used.

A correction factor of 1.023 was used to adjust the lengths of preserved fish before the regression equations of the body-scale relation used for back calculation of lengths were computed. This factor was determined by measuring 38 lake whitefish (250–400 mm long), 105 bloaters (100–250 mm), and 49 hybrids (100–300 mm) on the date of death and after preservation in 10% formalin for 1–3 years, when shrinkage had stabalized (Parker, 1963). Marked fish were measured alive at time of scale removal.

Cellulose acetate impressions were made of all scales (Smith, 1954) and examined at a magnification of 41× on a microprojector (Moffett, 1952). Two to five scales were examined from each unmarked fish and one or two scales for each date of removal from the marked fish. Application of several drops of acetone to the plastic strip, before impressing the scales, increased the clarity of the magnified image. Designation of age-groups followed the conventional practice which assumes that a fish becomes 1 year older on January 1 (Hile, 1936).

All fish were always fed as much as they would eat and all ate throughout the year.

TABLE I. Numbers of scale samples taken from various species of marked coregonids and periods of collection.

Species and year-class	Specimen no.	Period of collection	No. of months lived after marking[a]	No. of scale samples taken
Lake whitefish				
1962	1	9/14/62–5/1/63	8	4
1962	2	9/17/62–1/27/64	17	12
1962	3	9/17/62–12/10/63	16	9
1962	4	7/3/63–1/24/64	7	7
1959	5	6/8/62–12/10/63	19	17
1958	6	6/8/62–1/25/63	8	7
1958	7	6/8/62–2/28/64	21	16
Bloater				
1961	8	6/11/62–4/8/63	11	10
1961	9	7/5/63–3/7/64	9	8
1960	10	7/9/62–5/28/63	11	12
Lake herring × bloater hybrid				
1961	11	6/11/62–9/14/62	4	3
1961	12	6/13/62–1/15/63	8	7
1961	13	10/15/62–7/5/63	10	8
1961	14	8/9/63–2/6/64	7	6
Kiyi				
1961	15	6/8/62–4/8/63	11	8
1961	16	7/10/62–9/17/63	15	13
Total				137

[a]Includes months of marking and death.

The temperature of the spring water at the Northville station was 50 F (10 C). The water was sprayed into a large cement raceway and then pumped to the rearing troughs and tanks, or was taken by gravity feed from a large holding pond. Daily water temperatures for each tank were averaged by 10-day intervals.

A detailed account of methods, data, and analyses is given in the thesis upon which this paper is based (Hogman, MS, 1965).

TIME OF ANNULUS FORMATION

Almost all the scales had two strong marks each year, more than could be accounted for as annuli. The diameter increments within the two most recent marks and the total anterior-posterior diameter on each scale were measured along an imaginary line that passed through the focus and bisected the anterior and posterior fields (Van Oosten, 1929). After the scales of all groups of fish had been examined twice (randomly for each species) the percentage increase in scale diameter beyond the last mark was calculated for scales collected each month. The percentage increases for each fish were then arranged chronologically. Check formation was indicated when the percentage increase beyond the outermost mark dropped suddenly and then began to increase again.

A check that represented the true annulus (Fig. 1A, B) began to form on all species in late March 1963, and had usually circled the scale by mid-April. The earliest indication of annulus formation was on March 12, 1963, for a age-I whitefish. Annulus formation was not complete for some fish longer than 250 mm until late April. Fish entering their second through fourth growing seasons (age I–III) formed annuli slightly earlier than seven marked specimens age IV and older examined at or just after annulus formation.

All unmarked fish over 1 year old had the same pattern of dual marks on their scales for all years of life. The percentage increases in scale diameter beyond the outer mark could not be averaged for the unmarked fish because of the small number (1–3) available (that had died) each month for each species; and because of the great differences in growth of individual fish. However, direct observation of scales from unmarked fish collected before and after annulus and accessory check formation of the marked fish, indicated that they also formed their annulus in late March – early April and an accessory check in late October – early November.

Scales from fish that had ceased growing or were growing very slowly preceding annulus formation (three large whitefish and two bloaters) suggested that scale growth resumed before a measurable increase was detectable in the total length. The data did not permit evaluation of the relation of size within an age-group to time of annulus formation.

To determine the validity of annulus identification and provide further evidence for time of occurrence, the lengths of the marked fish were back-calculated for the 1962 and 1963 annuli and compared with known lengths at various dates. This method indicated that the 1962 annulus formed in March or April. The identification of the 1963 annulus, for all scales collected after April, was confirmed in like manner. Although fish were not marked until June 1962, they were measured monthly beginning in March 1962. By comparing the average back-calculated length (at the 1962 annulus) with the size of the largest fish in the tank for the months before June 1962, the March–April formation of the 1962 annulus was confirmed. The marked fish always maintained their size advantage over others in the tank after June 1962; therefore the assumption that they were also the largest during March to June seems warranted. A retention of size advantage has been demonstrated for brown trout (*Salmo trutta*) reared under artificial conditions (Brown, 1946).

The number of annuli on each fish corresponded to its age. Many fish exhibited highly distinct annuli (Fig. 1A and 3A), but most scales were more difficult to interpret. Often the year-mark was so faint it might have been overlooked on wild fish of unknown age.

TIME OF ACCESSORY CHECK FORMATION

An accessory check (Fig. 1, 3) was formed in the fall on scales of nearly all fish studied. Formation of the mark began in mid-October and was complete by mid-November.

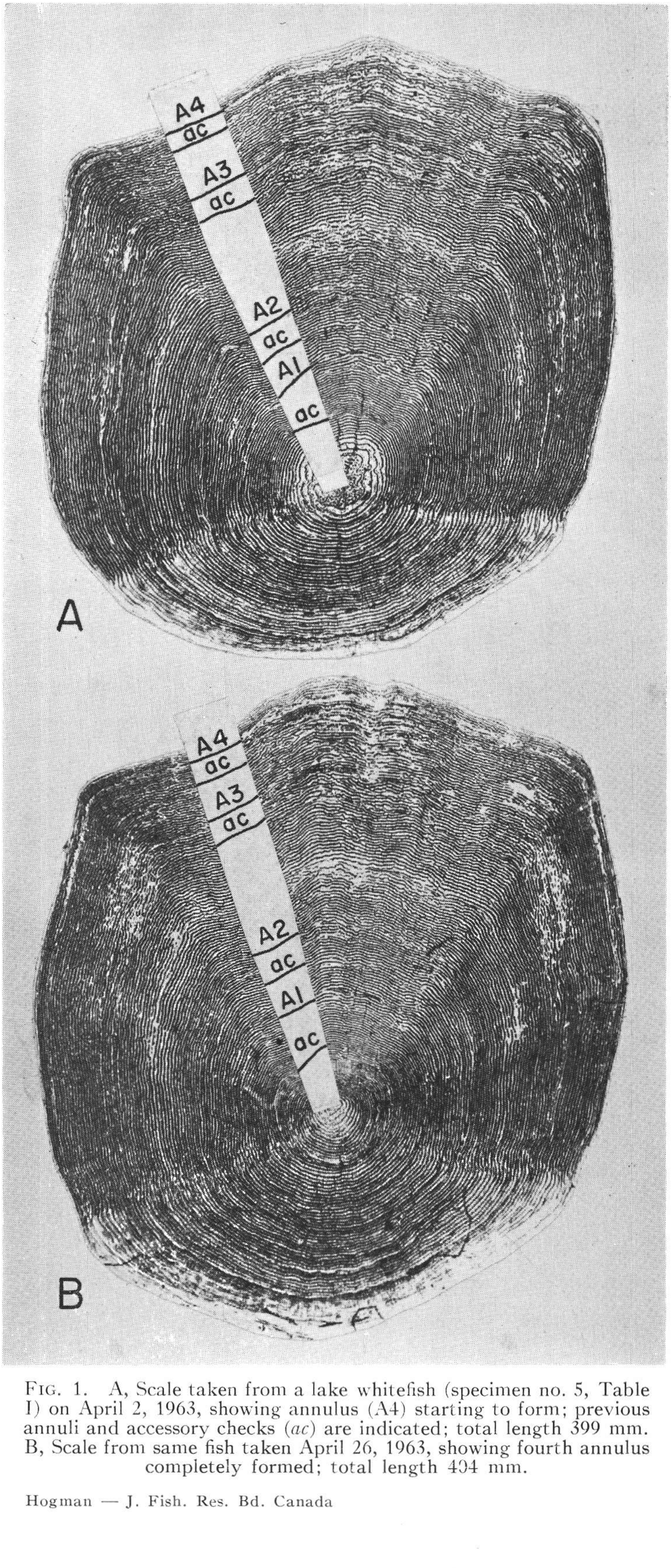

FIG. 1. A, Scale taken from a lake whitefish (specimen no. 5, Table I) on April 2, 1963, showing annulus (A4) starting to form; previous annuli and accessory checks (*ac*) are indicated; total length 399 mm. B, Scale from same fish taken April 26, 1963, showing fourth annulus completely formed; total length 404 mm.

FIG. 2. Scale taken from a lake whitefish (specimen no. 2, Table I) on September 17, 1962, before accessory check had formed; total length 114 mm.

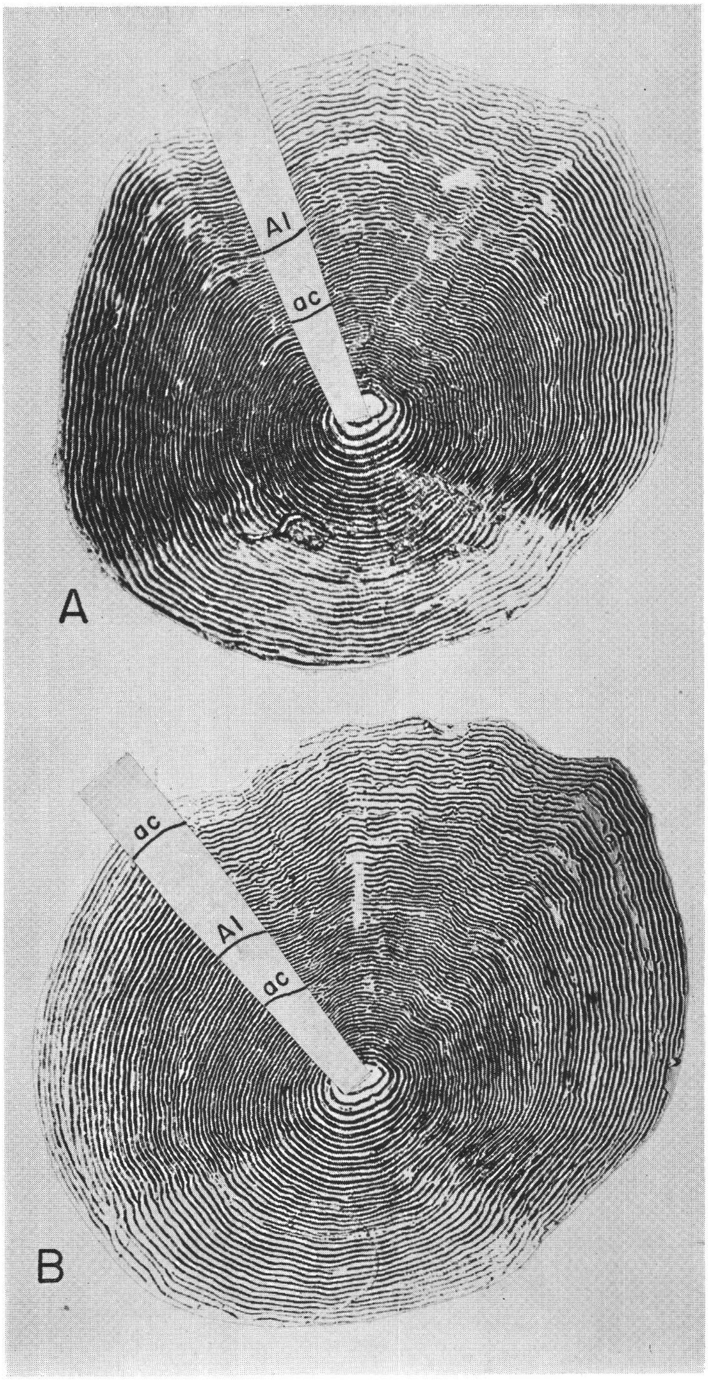

FIG. 3. A, Scale taken from a lake whitefish (specimen no. 2, Table I) on September 5, 1963, showing first accessory check and annulus; total length 246 mm. B, Scale from same fish taken on November 4, 1963, showing second accessory check completely formed; total length 264 mm.

The mark was absent (Fig. 2) on scales of three young-of-the-year whitefish in September 1962 but an accessory check had formed by early November. The first annulus formed in late March 1963. Scales from two of these fish that lived through the following fall showed only two strong marks (check and annulus) on September 5 (Fig. 3A) and October 7, but scales taken on November 4 had an additional strong check inside the margin (Fig. 3B).

The accessory check was not as well defined as the annulus but it could nearly always be detected. Comparison of calculated lengths from accessory checks with actual measurements in various months, verified the period when the checks were formed. Scales from unmarked fish that had died mid-November to January (all species and years) also had an accessory check just inside the margin. The widely spaced ridges between A2 and the next outer accessory check (*ac*) on Fig. 1 are commonly found in coregonid scales and reflect periods of fast growth (Van Oosten, 1923, 1929; Moffett, 1952). Seventeen sets of scales were taken from this fish (specimen 5, Table I) and they all showed the same characteristics and reflected very rapid growth during the early summer of 1961 at age II.

Accessory checks were not reported by Van Oosten (1923) on whitefish reared in the New York Aquarium, but they are known to occur for many lake populations of coregonids. Van Oosten (1929) illustrated a number of scales of lake herring from Lake Huron with marks between the annuli that I believe were accessory checks. Deason and Hile (1947) found that kiyis in Lake Michigan form definite annuli and prominent accessory checks on their scales despite small annual variation in water temperature (not over 2 or 3 degrees C) in the deep water where they live. Hile (1936) found that accessory checks occurred regularly on all scales of lake herring from Muskellunge Lake, Wisconsin, and Smith (1956) found false annuli on nearly all scales of Green Bay lake herring after the 2nd year of life. Barsukov (1960) described the annual formation of two rings on *Coregonus muksun*, a Russian whitefish.

Younger fish (ages 0–II) did not seem to form their accessory check earlier than older fish, although the check was more easily detected in young fish according to examinations of 10 marked fish and 34 unmarked fish. The clarity of the accessory check depended on the fish's growth rate after the check had formed. If the fish grew little after the late-October check formed on the scales, the check was faint and nearly indistinguishable on scales collected from November to January. If the fish did not grow after October, no scale material was deposited on the margin from November to March and an accessory check did not form. Of all the scales examined from marked fish, only three lake whitefish (larger than 400 mm, ages IV and V) and one bloater (241 mm, age II) failed to form an accessory check during 1 or more years.

GROWTH OF MARKED FISH

The marked fish grew fastest in the summer and slowest during the winter (Table II). The very largest fish in some groups showed no growth in length

TABLE II. Growth of various year-classes of marked fish in total length expressed as monthly percentage increases from annulus formation to annulus formation. Numbers of fish in parentheses; growth periods extend from the 16th day of one month to the 15th of the following month.

Period of growth	Lake whitefish			Bloater		Kiyi	Lake herring × bloater hybrid	Avg
	1958	1959	1962[a]	1960	1961	1961	1961	
1962–63								
Mar.–Apr.	6.1(2)	7.8(1)	–	4.6(1)	13.8(1)	9.5(2)	7.1(3)	8.2
Apr.–May	14.1(2)	8.7(1)	–	8.6(1)	14.2(1)	11.9(2)	8.4(3)	11.0
May–June	16.2(2)	11.0(1)	–	9.6(1)	10.8(1)	12.4(1)	12.1(2)	12.2
June–July	22.1(2)	11.0(1)	–	10.4(1)	9.7(1)	10.5(2)	14.6(3)	13.1
July–Aug.	21.2(2)	11.0(1)	–	18.2(1)	9.3(1)	9.5(2)	13.3(3)	13.8
Aug.–Sept.	14.2(2)	9.7(1)	–	15.4(1)	14.0(1)	9.3(2)	11.6(3)	12.4
Sept.–Oct.	6.1(2)	9.2(1)	4.6(3)	14.4(1)	14.7(1)	11.0(2)	8.0(3)	9.7
Oct.–Nov.	0.0(2)	6.6(1)	4.9(3)	8.8(1)	7.8(1)	6.0(2)	3.2(3)	5.4
Nov.–Dec.	0.0(2)	5.7(2)	4.9(3)	5.8(3)	2.9(1)	3.2(1)	4.2(3)	3.9
Dec.–Jan.	0.0(1)	6.6(1)	5.0(3)	1.9(1)	2.8(1)	4.8(2)	4.5(3)	3.7
Jan.–Feb.	0.0(1)	6.5(1)	3.2(3)	0.0(1)	0.0(1)	5.5(2)	5.2(3)	2.9
Feb.–Mar.	0.0(1)	6.2(2)	3.0(3)	2.3(1)	0.0(1)	6.4(2)	7.8(2)	3.7
1963–64								
Mar.–Apr.	–	–	4.9(3)	–	3.6(1)	–	10.5(2)	6.3
Apr.–May	–	–	7.2(5)	–	8.4(1)	–	11.2(2)	8.9
June–July	–	–	12.4(3)	–	18.9(1)	–	16.8(1)	16.0
July–Aug.	–	–	15.7(3)	–	15.7(1)	–	16.6(1)	16.0
Aug.–Sept.	–	–	14.0(3)	–	13.6(1)	–	11.6(1)	13.1
Sept.–Oct.	–	–	8.7(3)	–	8.6(1)	–	8.1(1)	8.5
Oct.–Nov.	–	–	8.5(3)	–	6.1(1)	–	3.6(1)	6.1
Nov.–Dec.	–	–	6.8(2)	–	1.9(1)	–	1.7(1)	3.5
Dec.–Jan.	–	–	5.3(2)	–	0.0(1)	–	1.8(1)	2.4
Jan.–Feb.	–	–	2.9[b]	–	2.7(1)	–	1.7(1)	2.4
Feb.–Mar.	–	–	3.7[b]	–	3.7(1)	–	3.7[b]	3.7

[a]Percentages for periods of growth in 1962–63 were obtained by dividing the amount of growth of each period by the growth to the first annulus.

[b]Data were not available for these months — the figures used are averages for corresponding periods of the 1962–63 growing season.

or on the scales during the winter. All others grew throughout the year; the slow winter growth did not cause cessation of scale growth, nor in most of the fish studied was the formation of accessory checks preceded or accompanied by a period of greatly reduced growth or no growth.

Data for whitefish used to illustrate growth covered the period September 1962 to December 1963 (Fig. 4). The annuli were formed at the start of a period of more rapid growth or during constant growth, and accessory checks were formed after the growth rate had become slower. The bloater, kiyi, and hybrid had growth curves similar to but somewhat more irregular than those of the whitefish. The irregularities for these species were random and could not be correlated with annuli or accessory marks on their scales.

As the size of the fish increased the rate of growth decreased, as is typical for whitefishes (Carlander, 1950). Growth of mature lake whitefish and bloaters was negligible over the winter. Two whitefish of the 1958 year-class (specimens no. 6 and 7) that matured in 1962 at age IV did not grow after late fall, and a whitefish of the 1959 year-class (specimen no. 5) that matured at age IV

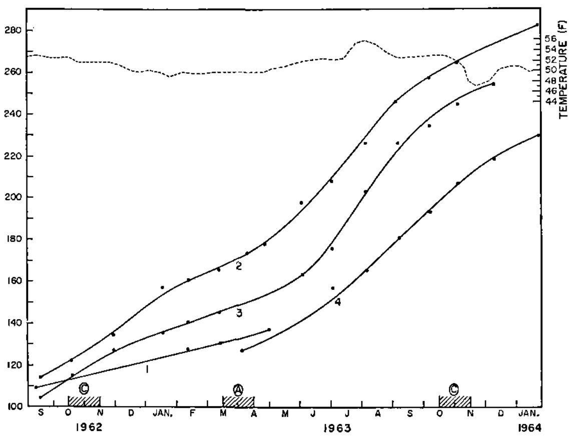

FIG. 4. Growth of four marked lake whitefish (1962 year-class) in 1962–64 and water temperature (broken line) in rearing tanks. Times of annulus formation (A) and accessory check formation (C) are indicated by circled letters. Numbers below curves are specimen numbers — see Table I.

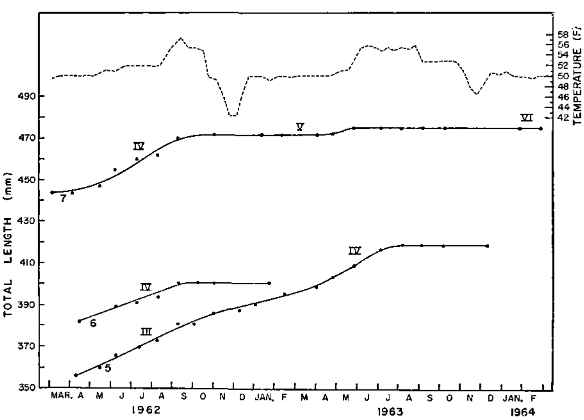

FIG. 5. Growth of lake whitefish (1958 and 1959 year-classes) in 1962–64 and water temperature (broken line in rearing tanks. Numbers below curves are specimen numbers — see Table I.

in 1963 did not grow after August 1963 (Fig. 5). The latter fish was growing at a nearly constant rate in March–May 1963 while its fourth annulus (Fig. 1) was forming.

BODY-SCALE RELATIONSHIP

None of the coregonids exhibited a constant body-scale ratio. The body-scale relationship for all species was described by a straight line; intercepts on the axis of length ranged from 34 to 46 mm. The relations between magnified (×41) scale diameter (S) and total length (L) in millimeters of marked and unmarked coregonids, year-classes combined, were:

Species	Equation
Lake whitefish	$L = 34 + 1.057\ S$
Bloater	$L = 46 + 1.003\ S$
Lake herring × bloater hybrid	$L = 36 + 1.041\ S$
Kiyi	$L = 34 + 0.947\ S$

Lengths were calculated from the formula:

$$L_n = a + \frac{(L_t - a)}{S_t} S_n$$

where L_n equals length of fish at annulus (or accessory check) n, L_t equals fish length at time of scale removal, a equals the total length intercept of the body-scale equation, S_t equals the total scale diameter, and S_n equals the scale diameter at annulus (or accessory check) n. The calculated length of a particular marked fish at annulus n agreed very closely (±1–3 mm) with its measured length when annulus n was formed, or with its measured length in March–April before the series of scale collections was started.

Although the length intercepts for lake whitefish, bloaters, and kiyi were entirely satisfactory for calculation of growth in my experimental stocks, I do not suggest that they are generally applicable. The body-scale relation is known to vary from population to population of the same species. In Lake Superior, for example, the body-scale regression for lake whitefish has an intercept on the length axis in the Munising Bay population (Edsall, 1960) but passes through the origin in the Apostle Islands stocks (Dryer, 1963).

EFFECTS OF TEMPERATURE, FOOD, AND LIGHT ON FORMATION OF ANNULUS AND ACCESSORY CHECK

The constancy of water temperature at 50 F (10.0 C) during time of annulus formation (Fig. 4 and 6) proves that changing temperatures were not necessary to initiate formation of an annulus on the scales. Van Oosten (1923) suggested that adult fish (age VIII and IX) stopped growing in the winter and that rising water temperature (from 39 to 45 F; 3.9 to 7.2 C) in March and April caused annulus formation on whitefish reared in the New

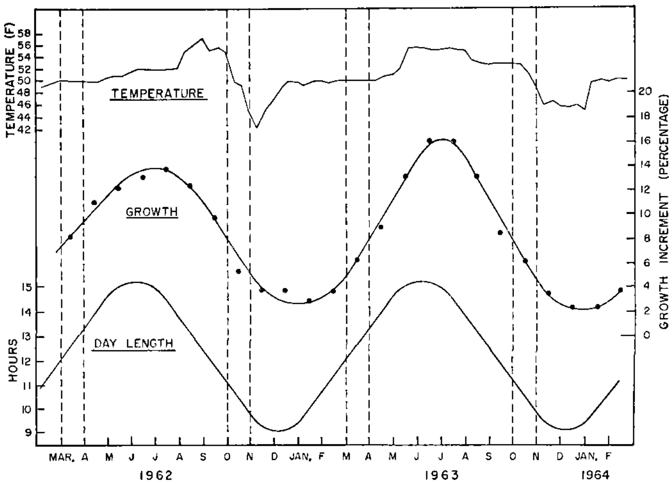

FIG. 6. Average monthly percentage increments of marked fish, hours of day length (sunrise to sunset), and average water temperatures, 1962–64. Periods of formation of annuli (March–April) and accessory checks (October–November) are indicated by vertical broken lines. Growth data from Table II.

York Aquarium. Only a few of the largest fish in the present study ceased growing during the winter.

During the period of accessory check formation, from mid-October to mid-November, water temperature decreased from 55.0 to 45.3 F (12.8–7.4 C) in 1962 and from 53.0 to 48.5 F (1.7–3.0 C) in 1963. The decrease during the same period was much less in 1958–61, however, and in some years it was less than 1 F (0.6 C): 53.6–51.2 F in 1958; 52.0–51.7 F in 1959; 52.8–52.0 F in 1960; and 51.9–49.4 F in 1961. Since all fish that were growing formed accessory checks in all years, it seems unlikely that temperature change alone may have caused formation of the accessory check.

In November 1962 and 1963 colder water from the holding pond was added to the water pumped into the tanks that held mature fish, to simulate water-temperature changes experienced by wild fish during the spawning period, but the changes (Fig. 5) came after the accessory checks had already formed. Cold water was not pumped into the tanks that held the immature fish of ages 0 and I (all species and year-classes). Consequently, they experienced less temperature variation in the fall (Fig. 4 for 1962); temperature did not fall below 49 F (9.4 C) for age 0, or 47 F (8.3 C) for age I. The use of spring water exclusively after the spawning period in mid-December kept the water temperature for all fish at 50 ± 0.3 F (10.0 ± 0.2 C) until late April or early May.

Neither the kind nor quantity of food was changed during the periods of formation of annuli and accessory checks, and no changes were observed in feeding during these periods. Mature whitefish ate less food during their spawning period, but spawning came after the check had formed. Mature whitefish shorter than 400 mm resumed normal feeding after spawning; those longer than 400 mm did not feed as actively.

Prophylactic inoculations of chloroamphenicol and sulfa drugs, administered monthly, could not be correlated with the formation of marks on scales.

Seasonal change in growth rate of the marked coregonids was much more closely related to day length (hours from sunrise to sunset) than to changes in water temperature (Fig. 6) or any other known factor. Monthly increments were lowest in late December to early February, when periods of daylight were shortest. The annulus did not begin to form until mid-March, when periods of daylight had started to lengthen. Separate growth curves for the marked whitefish of the 1962 year-class (Fig. 4) show more clearly the actual growth of most fish studied. The fall accessory check on the marked fish formed during a period of decreasing growth but the decrease was not sudden, nor was it followed by rapid growth after check formation.

The day length that coincided with the periods of mark formation was 12.1 hr in the spring and 11.0 hr in the fall. The fall mark formed 1–2 months before the minimum day length of 9.1 hr in late December and the annulus formed near the middle of the period of rapid increase in day length (Fig. 6). No attempt was made to control seasonal variations in light, or light in the tank room. The internal illumination from electric lights did not dominate the natural light entering the large windows surrounding the tank room.

AN EXPLANATION OF FORMATION OF MARKS

The formation of a spring mark during a period of increasing growth or small change in growth, and a fall mark during a period of declining growth or little change in growth is contrary to the usual assumption that a mark forms at the onset of rapid growth after a period of reduced or no growth. It has also been widely assumed that temperature, through its effect on a fish's metabolic rate, is the principal factor of annulus formation (e.g., Graham, 1928; Beckman, 1943; Lagler et al., 1962).

An increase in fish length may determine the increase in the scale diameter but the pattern of circuli may be governed by additional factors. Wallin (1957) discussed the development of scale markings in considerable detail. He showed that the circuli are caused by calcification of ridges produced by pressure of the scale against the scale pocket. The periphery of the scale is proteinaceous and subject to formation of pressure ridges. As additional protein is deposited around the scale, the ridges are farther from the edge and become impregnated with inorganic salts. A typical single ridge (or circulus) begins to form and is calcified along the anterior region (imbedded part of the scale), and then continues to form and calcify posteriorly around the lateral edges of the scale until the ends meet along the posterior margin. As many as 3–10 circuli can be in various stages of completion at one time. If protein deposition stops or is reduced the incomplete ridges calcify to their tips. Keeton (1965) demonstrated that the proteinaceous margin (Wallin's ossoid growth zone) may not become reduced when the rate of protein deposition is temporarily retarded or arrested, but the calcification of the ridges continues. If the proteinaceous growth resumes, the incomplete ridges do not resume their encircling growth, but a new ridge begins to form at the anterior edge, proceeds around the lateral edges, and eventually encircles the scale. This new ridge "cuts across" the incomplete circuli to complete the annulus characteristic of coregonids and many other fishes.

Possibly a physiological protein-demand cycle existed in the laboratory-reared coregonids that caused a periodic diversion of scale protein to support other metabolic functions. A biannual cycle would explain formation of annuli and accessory checks without a cessation in fish growth.

When coregonids become ripe in the fall, their gonad development may create a high protein demand. Many fish of the 1958 year-class that spawned in 1962 and 1963 showed evidence of scale resorption in late summer and fall, which suggests the diversion of scale protein. Immature fish did not show scale resorption in the fall but apparently experienced a sufficient change in their protein-deposition rate to form the characteristic accessory check.

The formation of an annulus in the spring may also reflect a metabolic change during the period that growth was increasing or nearly constant, but the reasons are unknown. Conceivably, the demand could be generated by increased activity during the time of rapidly lengthening days.

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